

# Insects from the Early Eocene amber of Oise (France): diversity and palaeontological significance

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**Abstract:** A general state of the art of entomofaunistic studies of the Eocene Oise amber is presented. Even though several orders have already been the subject of extensive studies, many things remain to be done, especially in the Lepidoptera, Trichoptera, Ephemeroptera, and Blattodea, orders of great importance for palaeoenvironmental reconstructions. At the present stage of knowledge, few taxa are shared by the Oise and the younger Baltic amber. This is probably due to rapid changes and evolution in the insect taxa during the Early Eocene, maybe in relation to the great global climatic degradations occurring after the maximum warming of the Late Paleocene.

**Key words:** Amber deposit, Eocene, Insects, faunistic changes.

**Santrauka:** Straipsnyje bendrai aptariami eoceninio Oise (Pranc zija) gintaro entomofaunos tyrimai. Nors keletas vabzdžių būrių yra plačiai tiriama, tačiau dar daug kas neiširta, ypač Lepidoptera, Trichoptera, Ephemeroptera ir Blattodea būriai, kurie yra itin svarbūs paleoaplinkai rekonstruoti. Dabar žinomi keli vabzdžių taksonai, bendri Oise ir jaunesniam Baltijos gintarui. Tai, matyt, yra susiję su greitais vabzdžių taksonų pokyčiais ir evoliucija ankstyvajame eocene, kuriuos tikriausiai sukėlė didžiulė globalinė klimato degradacija, susidariusi po maksimalaus vėlyvojo pleistoceno atšilimo.

**Raktiniai žodžiai:** Gintaro telkinys, eocenas, vabzdžiai, faunos pokyčiai.

## Introduction

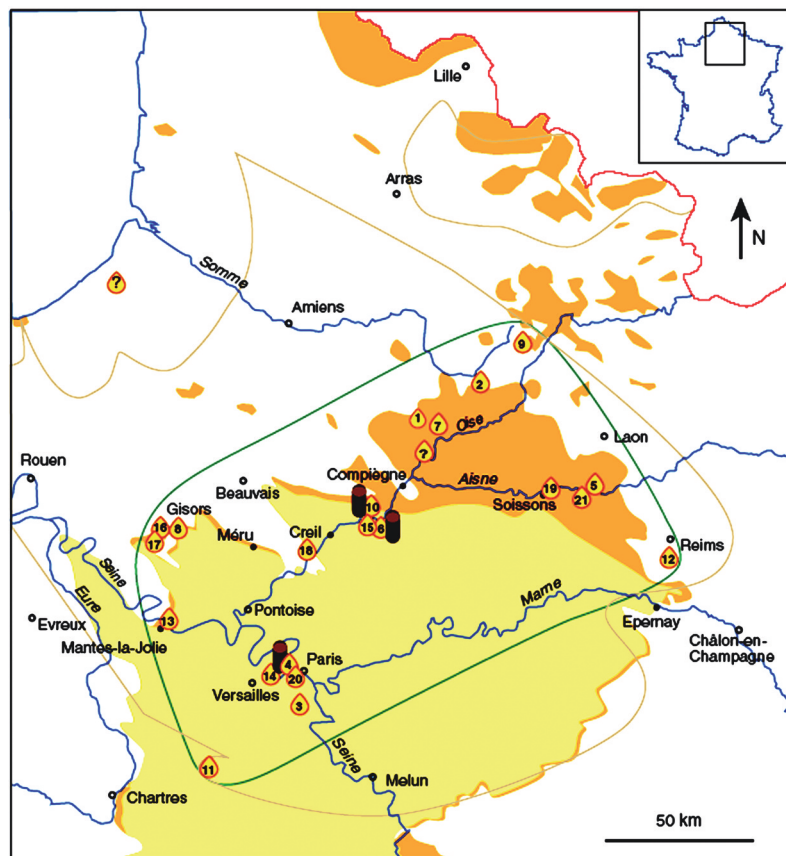
The amber deposit of Oise has been recently discovered by Gael DE PLOËG (NEL et al. 1999) in 1996. This deposit is located near Creil at the place known as "Le Quesnoy" (Creil, Oise, France). The lignite layers containing the amber are from the Lower Eocene of the Paris basin (~53 Ma). The strata, typical "Argiles à lignite du Soissonnais" are at the bottom of two channels cutting into the underlying Thanetian marine green sands (Table 1, Fig. 1). These Sparnacian beds are made up of a succession of lenticular bodies showing two main facies: clayey sands rich in frequently pyritised lignite, together with amber; and grey clayey sands with less lignite (1-12% of the sediment). These facies reflect a hypoxic environment.

At this time, a global warming period caused a relative mass extinction in Europe (HARRINGTON & JAMARILLO 2007) but this extinction apparently did not affect the insects. High temperatures and warm oceans created a mild and humid environment (PEARSON et al. 2001), which enabled the "tropical" forests to grow in Europe. In Oise, the dominance of an arborescent amber-producing species and the presence of freshwater suggest a semi-deciduous forest (NEL et al. 2004b). The climate at that time was hot with a wet season, which

corresponds to a sub-tropical climate (DE FRANCESCHI & DE PLOËG 2003). The producing amber tree is *Aulacoxylon sparnacense* (Combretaceae or Caesalpiniaceae) which could be close to the extant plants *Terminalia* L. (Combretaceae) or Leguminosae-Caesalpiniaceae (DE FRANCESCHI & DE PLOËG 2003).

Ten tons of soil have been sorted to extract amber (about 350 kg) (NEL et al. 1999). The deposit contains a high diversity of vertebrate fauna. The collected material relates to dental and skeletal remains, many coproliths and a few exceptional items preserved in amber (hair, feathers) and in coproliths (bones, teeth, fingerprints, skin) (NEL et al. 1999). A collection of 15,000 arthropods divided into more than 300 morphospecies (NEL et al. 1999) already existed in 1999. Up to date, 20,000 inclusions in amber have been collected; additional forms of arthropods have been recognized. They are mainly hexapods, mites, spiders and two pseudoscorpions. Scorpions and myriapods are still unrecorded (NEL et al. 2004).

We present hereafter an inventory of insects already described from the deposit of Oise. We discuss the originality of the collection and further perspective.



**Fig. 1:** Map of deposit of *Aulacoxylon sparnacense* COMBES, 1907 and Sparnacian amber (according to DE FRANCESCHI & DE PLOËG 2003).

## Results

Seventeen orders have already been identified: Blattodea, Coleoptera, Dermaptera, Diptera, Ephemeroptera, Hemiptera (including Heteroptera), Hymenoptera, Isoptera, Lepidoptera, Mantodea, Megaloptera, Neuroptera, Odonata, Orthoptera, Psocoptera, Thysanoptera, and Trichoptera (Table 2). Seventy-nine species have been described from the deposit (Table 2) belonging to 49 different families with a significant proportion of Coleoptera, Hymenoptera and Psocoptera but a few Diptera, Dermaptera, and Megaloptera (Table 2, Fig. 2). We detail hereafter the palaeontological significance of the species described from Oise.

### Blattodea

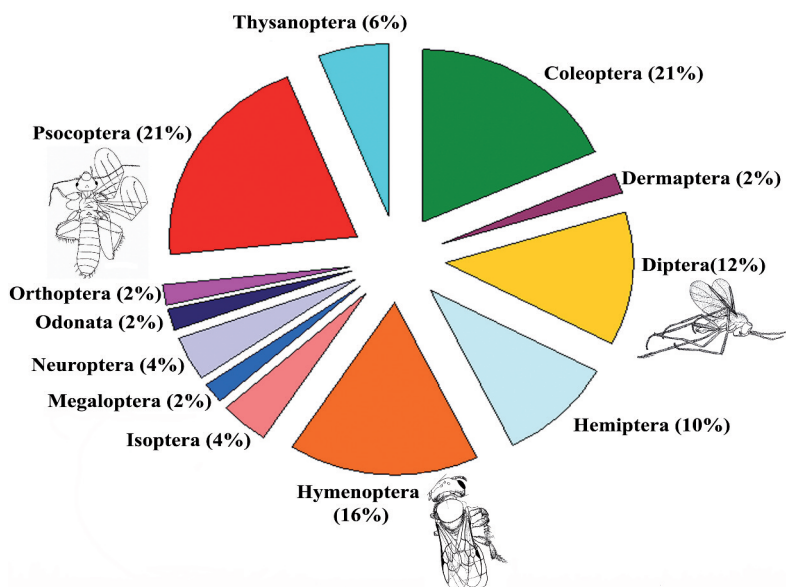
These insects are rather diverse with some very particular forms, suggesting a high diversity of chorologies. The whole material remains to be studied.

### Coleoptera

The new species *Macroisagon deuvei* is the second representative fossil of the extant genus of *Macroisagon* HENTZ, 1830 (Fig. 3D) (BATELKA et al. 2006). Ripiphoridae are rather rare in the fossil records, with Cenozoic taxa described or cited from the Eocene Baltic amber, the Oligocene of Germany, and the Miocene Dominican amber (KAUPP et al. 2001). The Mesozoic record comprises one species from the Burmese amber and two from France (PERRICHOT et al. 2004).

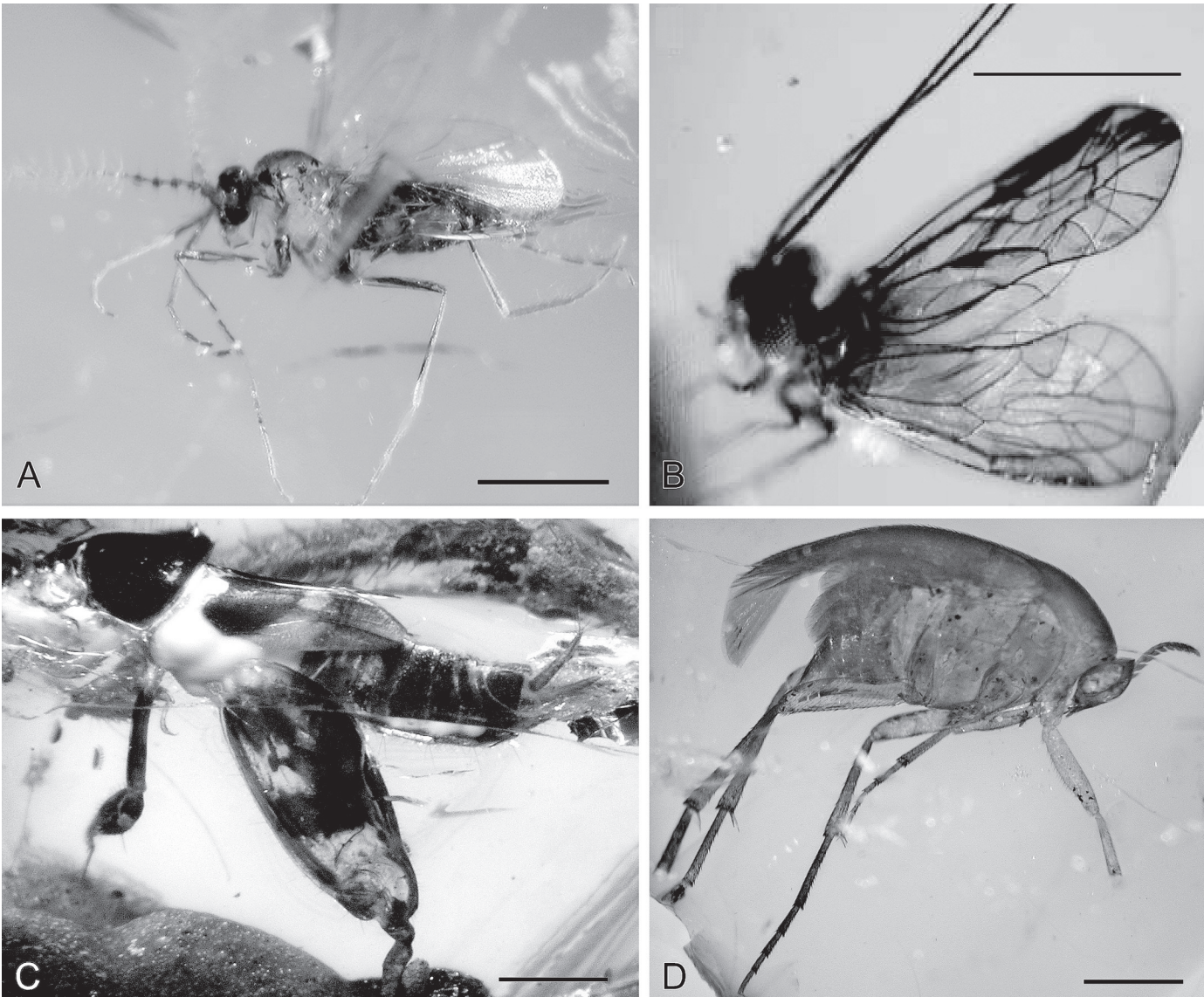
Two new species of Archostemata, *Cupes ponomarenkoi* (Cupedidae) and *Micromalthus eocenicus* (Micromalthidae) have also been described, the latter representing the oldest member of genus *Micromalthus* LECONTE, 1878 (KIREJTSHUK et al., in press).

Three new genera, one new subgenus and 11 new species of the superfamilies Scirtoidea, Cleroidea, and Cucujoidea (suborder Polyphaga) originated from this lowermost Eocene amber, namely: the Scirtidae *Cyphon gallicus* and ?*Cyphon lobanovi*; the Melyridae: Malachiinae ?*Colotes constantini* and ?*C. implexus*; the Nitidulidae: Cybocephalinae *Cybocephalus* (*Macromethaponus*)



**Fig. 2:** Relative family diversity among insect orders found in Oise amber (n = 37). Representative figures: Hymenoptera = *Paleomacropis eocenicus* MICHEZ & NEL, 2007; Psocoptera = *Embidopsocus eocenicus* NEL, DE PLOËG & AZAR, 2004; Diptera = *Lestremia eocenica* NEL & PROKOP, 2006.



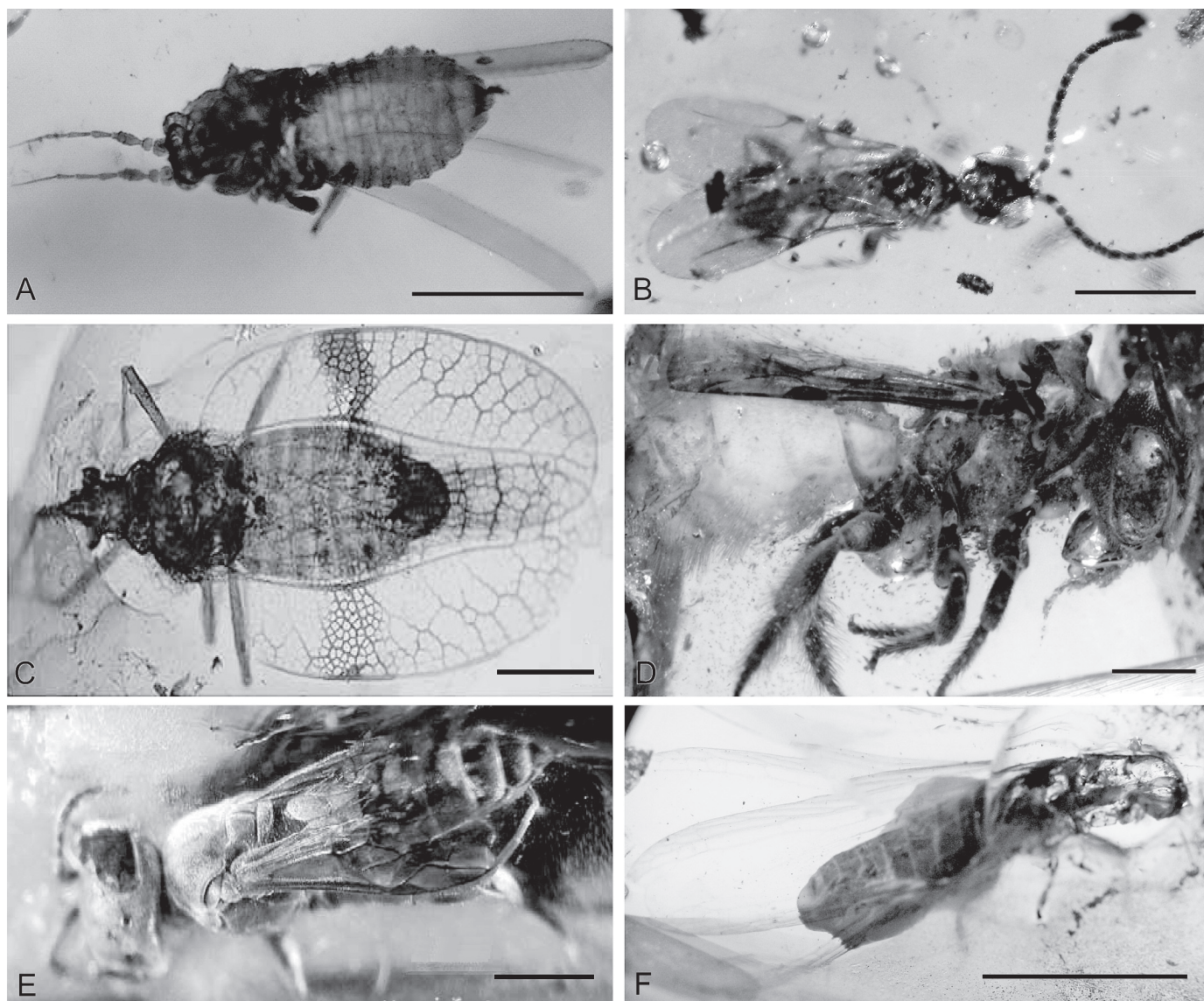


**Fig. 3:** Insects described from the French amber of Oise. A. Diptera, *Lestremia deploegi* NEL & PROKOP, 2006 (scale = 1 mm); B. Psocoptera, *Eolachesilla eocenica* NEL et al., 2005 (scale = 1 mm); C. Orthoptera, *Guntheridactylus grimaulti* AZAR & NEL, 2008 (scale = 800 µm); D. Coleoptera, *Macrosiagon devei* BATELKA et al., 2006 (scale = 1 mm).

**Table 1:** Stratigraphy and lithology in the Oise region (Lower Eocene). The amber occurs in the lower Sparnacian lignite.

|                 |                   |        |  |                |
|-----------------|-------------------|--------|--|----------------|
| <b>Ypresian</b> | <b>Cusian</b>     | Upper  | 1. Clay of Laon – Stoneway of Fosse and Belleu – Sand of Glennes – Sand with unios and teredines.<br>2. Sand of Hérouval – Sand of Cuise – Sand of Pierrefonds |                |
|                 |                   | Lower  | Sand of Aizy   |                |
|                 |                   | Basal  | Tuffeau of Mont-Notre-Dame<br>Sand of Laon<br>Varengeville's Formation   |                |
|                 | <b>Sparnacian</b> | Upper  | Stoneway of Bruyère-la-Comtesse, Urcel and Chaillevois<br>Faluns with cyrenes and oysters ("false clay")   |                |
|                 |                   | Medium | Sand of Sinceny  | Clay of Sarron |
|                 |                   | Lower  | Sand of Auteuil  |                |
|                 |                   |        | Soissonais clays and brown lignite<br>Vaugirard's plastic clays  |                |
|                 |                   | Basal  | Limestone of Clairoux, Mortemer and Cap d'Ailly<br>Marl of Sincery, Dormans, Chenoy, Lamrolaye and Montgiroux<br>Conglomerate of Meudon                        |                |





**Fig. 4:** Insects described from the French amber of Oise (continued). A. Thysanoptera (scale = 250  $\mu$ m); B. Hymenoptera, *Rhabdepyris gallicus* PERRICHOT & NEL, 2008 (scale = 500  $\mu$ m); C. Hemiptera, *Parazetekella eocenica* NEL, WALLER & DE PLOËG, 2004 (scale = 1 mm); D. *Paleomacropis eocenicus* MICHEZ & NEL, 2007 (scale = 800  $\mu$ m); E. Hymenoptera, *Eopison menieri* NEL, 2005 (scale = 1 mm); F. Isoptera, *Electrotermes flecki* NEL et al., 2006 (scale = 4 mm).

*longifrons*, *Pastillocenicus fossilis*, and *P. grandiclavus*; the Kateretidae: *Hetherelus expressus* and *Eoceniretes yantaricus*; the Smicripidae: *Smicrips europeus*; and the Anthicidae: Eurygeniinae *Oisegenius antiquus* (KIREJTSHUK & NEL 2008).

### Dermaptera

Earwigs are very scarce in the insect fossil record. NEL et al. (1994) listed only 73 taxa of Dermaptera described in the literature, ranging in age from the Lower Jurassic to the Pleistocene. Among them, only nine species are described from Baltic amber, Burmese amber, Dominican amber and Saxonian amber (NEL et al. 2003). The fossil record stands at about 83 species against some 2,000 modern species. The newly species

described from the lowermost Eocene amber of the Paris basin shows a unique structure of the cerci with tuft of spiny hairs. Its phylogenetic position is not yet resolved (NEL et al. 2003b).

### Diptera

New genera and twelve species have been described from the Early Eocene amber of Oise (Table 2), which are included in five extant families: Bibionidae, Bombyliidae, Cecidomyiidae, Psychodidae, and Scatopsidae.

Although Bibionidae are frequent in the Cenozoic lacustrine deposits, they are rare in amber (GEE et al. 2001). WEITSCHAT & WICHARD (1998) indicated that the Bibionidae represent between 0.03 and 0.2% of the Diptera, Nematocera in Baltic amber, GRIMALDI &

**Table 2:** Insect taxa described from Oise amber. Number of families and species in brackets.

| Taxon  | References            |
|--|-----------------------|
| <b>COLEOPTERA (9 – 14)</b>   |                       |
| Anthicidae: <i>Oisegenius antiquus</i>   | KIREJTSHUK & NEL 2008 |
| Cupedidae: <i>Cupes ponomarenkoi</i>   | KIREJTSHUK & NEL 2008 |
| Kateretidae: <i>Hetherelus expressus</i> , <i>Eoceniretes yantaricus</i>   | KIREJTSHUK & NEL 2008 |
| Melyridae: ? <i>Colotes constantini</i> , ? <i>C. implexus</i>   | KIREJTSHUK & NEL 2008 |
| Micromalthidae: <i>Micromalthus eocenicus</i>  | KIREJTSHUK & NEL 2008 |
| Nitidulidae: <i>Cybocephalus longifrons</i> , <i>Pastilloecenicus fossilis</i> , <i>P. grandiclavus</i>  | KIREJTSHUK & NEL 2008 |
| Ripiphoridae: <i>Macrodiagonea deuvei</i>  | BATELKA et al. 2006   |
| Scirtidae: <i>Cyphon gallicus</i> , ? <i>Cyphon lobanovi</i>   | KIREJTSHUK & NEL 2008 |
| Smicripidae: <i>Smicrips europeus</i>  | KIREJTSHUK & NEL 2008 |
| <b>DERMAPTERA (1 – 1)</b>  |                       |
| ?, <i>Chelisoficula caussaneli</i>   | NEL et al. 2003b      |
| <b>DIPTERA (6 – 12)</b>  |                       |
| Bibionidae: <i>Plecia parisiensis</i>  | GEE et al. 2001       |
| Bombyliidae: <i>Elektrophthiria magnifica</i>  | NEL 2006              |
| Bombyliidae: <i>Paradolichomyia eocenica</i>   | NEL et al. 2004       |
| Cecidomyiidae: <i>Lestremia eocenica</i> , <i>L. deploegi</i> , <i>Neurolyga magnifica</i> ,<br><i>Procoenonia olgae</i> , <i>Electroxylomyia eocenica</i> | NEL et al. 2006       |
| Mythicomyiidae: <i>Eurodolipteryx inexpectatus</i>   | NEL 2006              |
| Mythicomyiidae: <i>Proplatypygus matilei</i>   | NEL et al. 2004       |
| Psychodidae: <i>Eotrichomyia electronica</i>   | NEL et al. 2002       |
| Scatopsidae: <i>Cookella eocenica</i>  | NEL et al. 2004       |
| <b>HEMIPTERA (5 – 10)</b>  |                       |
| Achilidae: <i>Angustachilus longirostris</i> , <i>Cixidia christinae</i>   | LEFEBVRE et al. 2007  |
| Cixiidae: <i>Balticixius insignis</i>  | LEFEBVRE et al. 2007  |
| Cixiidae: <i>Stalisyne lutetiorum</i> , <i>S. veromanduorum</i> , <i>Mnaomaia bellovaciorum</i> ,<br><i>Mnasthaia arverniorum</i>                          | SZWEDO et al. 2006    |
| Piesmatidae: <i>Eopiesma trimerum</i>  | NEL et al. 2004c      |
| Thaumastocoridae: <i>Protodoris minusculus</i>   | NEL et al. 2004e      |
| Tingidae: <i>Parazetkella eocenica</i>   | NEL et al. 2004d      |
| <b>HYMENOPTERA (8 – 12)</b>  |                       |
| Aulacidae: <i>Aulacus eocenicus</i>  | NEL et al. 2004f      |
| Bethylidae: <i>Protobethylus eocenicus</i>   | DE PLOËG et al. 2004  |
| Bethylidae: <i>Rhabdepyris gallicus</i> , <i>Elektroepyrus magnificus</i>  | PERRICHOT & NEL 2008  |
| Dryinidae: <i>Pseudodryinus parisiensis</i>  | PEINADO et al. 2006   |
| Ichneumonidae: <i>Palaeometopius eocenicus</i>   | MENIER et al. 2004    |
| Melittidae: <i>Paleomacropis eocenicus</i>   | MICHEZ et al. 2007    |
| Scelionidae: <i>Galloscelio pumilio</i> , <i>Moravoscelio bednariki</i>  | NEL et al. 2005       |
| Scolecbythidae: <i>Eobythus patriciae</i>  | LACAU et al. 2000     |
| Sphecidae: <i>Eopison menieri</i> , <i>Pison eocenicus</i>   | NEL 2005              |
| <b>ISOPTERA (2 – 2)</b>  |                       |
| Kalotermitidae: <i>Electrotermes flecki</i>  | NEL et al. 2006       |
| Mastotermitidae: <i>Mastotermes minutus</i>  | NEL et al. 2006       |
| <b>MEGALOPTERA (1 – 1)</b>   |                       |
| Sialidae: <i>Eosialis dorisi</i>   | NEL et al. 2001       |
| <b>NEUROPTERA (2 – 2)</b>  |                       |
| Rhachiberothidae: <i>Eorhachiberotha celinea</i>   | NEL et al. 2005a      |
| Sisyridae: <i>Paleosisyra eocenica</i>   | NEL et al. 2003a      |
| <b>ODONATE (1 – ?)</b>   |                       |
| Libellulidae   | FLECK et al. 2000     |
| <b>ORTHOPTERA (1 – 1)</b>  |                       |
| Tridactylidae: <i>Guntheridactylus grimaulti</i>   | AZAR & NEL 2008       |
| <b>PSOCOPTERA (10 – 11)</b>  |                       |
| Amphientomidae: <i>Amphientomum parisiensis</i>  | NEL et al. 2005b      |
| Archipsocidae: <i>Archipsocus</i> cf. <i>puber</i>   | NEL et al. 2005b      |
| Empheriidae: <i>Empheria intermedia</i>  | NEL et al. 2005b      |
| Lachesillidae: <i>Eolachesilla eocenica</i>  | NEL et al. 2005b      |
| Lepidopsocidae: <i>Thylacella eocenica</i>   | NEL et al. 2005b      |

**Table 2:** continued.

| <b>Taxon</b>   | <b>References</b>        |
|--|--------------------------|
| <b>PSOCOPTERA (continued)</b>  |                          |
| Liposcelididae: <i>Embidopsocus eocenicus</i>                                    | NEL et al. 2005b         |
| Manicapsocidae: <i>Eomanicapsocus melaniae</i> , <i>Eoprotoctopsocus celinea</i> | NEL et al. 2005b         |
| Pachytroctidae: <i>Tapinella eocenica</i>  | NEL et al. 2005b         |
| Psoquillidae: <i>Eorhyopsocus magnificus</i>                                     | NEL et al. 2005b         |
| Psyllipsocidae: <i>Psyllipsocus eocenicus</i>                                    | NEL et al. 2005b         |
| <b>THYSANOPTERA (3 – 13)</b>   |                          |
| Phlaeothripidae  | NEL et al., unpubl. data |
| Melanthripidae   |                          |
| Thripidae  |                          |

CUMMING (1999) recorded Bibionidae in Canadian amber, MEUNIER (1899, 1907) also recorded Bibionidae in Baltic amber and HARDY (1971) recorded one in Mexican amber.

Bombyliid flies are not rare in the fossil record, with 33 described genera and 51 species (EVENHUIS 1991, 1994). A fossil fly with a rounded head and a long neck has been described in the Early Eocene amber of Oise (NEL et al. 2004). The known fossils are mainly from the Late Eocene, Oligocene or Miocene. Cretaceous and early Cenozoic bee flies are much less frequent (NEL 2006).

Several new genera and species showing that Cecidomyiidae diversity was already rather high in the Early Eocene (Fig. 3A) (NEL et al. 2006). Fossil remains of Cecidomyiidae are frequent in Late Eocene Baltic and Rovno ambers, Oligocene Mexican amber and Late Cretaceous amber (MEUNIER 1904; GAGNÉ 1973, 1977; ARILLO et al. 2000; PERKOVSKI et al. 2004; FEDOTOVA 2004, 2005). There are a few morphological differences between these Early Eocene fossils and the corresponding Recent taxa (NEL et al. 2006). Nevertheless, the most diverse Recent subfamily Cecidomyiinae is still unrecorded in the Oise amber.

The superfamily Psychodoidea is one of the best known among the dipteran fossil records (52 species in 18 genera) (EVENHUIS 1994; AZAR et al. 1999). Specimens from the Early Eocene amber of Oise bring new informations about systematics of the family.

Scatopsidae (Nematocera) is a small group with a poorly known fossil record. AMORIM (1998) recognized 14 fossil species mainly from amber, POINAR & MILKI (2001) found an undescribed specimen from the Lower Cretaceous Lebanese amber, RASNITSYN & ROSS (2000) found an undescribed Scatopsidae from upper Albian Burmese amber (Myanmar), GRIMALDI (2000) found undescribed specimens from Turonian amber of New Jersey, and PIKE (1994) discovered also specimens from the Upper Cretaceous Grassy Lake amber.

## Ephemeroptera

Only adults have been found. The great majority of the specimens belong to one small undescribed species of Baetidae. Only three other undescribed species have been recognised. Such a faunistic spectrum suggests that the amber producing forest was not far from freshwater sources, but probably not very close to them.

## Hemiptera

The family Cixiidae SPINOLA, 1838 has a fossil record extending back to the Early Cretaceous and it is one of the most common groups in the Eocene Baltic amber (SZWEDO et al. 2006). The fossil taxa described from Oise amber (LEFEBVRE et al. 2006; SZWEDO et al. 2006) are very important in the reconstitution of phylogenetic scenarios among Cixiidae.

The Heteroptera described (Piesmatidae, Thaumastocoridae and Tingidae) are not very frequent in the fossil record. Piesmatidae is a small family of Lygaeoidea including six modern genera (NEL et al. 2004c). The former family was not represented in the fossil record except one citation of an undescribed specimen from the Upper Cretaceous Burmese amber (GRIMALDI et al. 2002) and a fossil from the Upper Eocene Baltic amber.

Thaumastocoridae includes six extant genera and only three described fossil species from the Dominican and Baltic amber (POINAR et al. 1997; BECHLY et al. 2000; SLATER et al. 2000). Their record in the Paris basin during the lowermost Eocene supports the occurrence of a very warm seasonal climate (NEL et al. 2004e).

New Tingidae from the lowermost Eocene amber of the Paris basin (Fig. 4C) represent the second oldest accurate record of the family, the oldest being from the mid-Cretaceous (NEL et al. 2004d; PERRICHOT et al. 2006).

## Hymenoptera

Hymenoptera is the third most diverse order in the Oise amber after the Coleoptera and Psocoptera (Fig. 2). Eight families have been discovered and ten new species. All the species are related to extant families.



Aulacidae are rare in the fossil record with about 20 described species (NEL et al. 2004f). The Cenozoic record of this group comprises species from the Upper Eocene of the Isle of Wight, Baltic amber and from the Oligocene of North America (NEL et al. 2004f).

Bethylid wasps are not very frequent in the fossil record (DE PLOËG et al. 2004), this family is mainly known from the Copal of Zanzibar (KROMBEIN 1992), the Lower Miocene Dominican amber, the Oligocene amber of Chiapas (Mexico) (GORDH et al. 1990), the Upper Eocene lacustrine beds of the Isle of Wight (UK) and Baltic amber (BRUES 1932; POLASZEK & KROMBEIN 1994; OHL 1995), the uppermost Cretaceous Burmese amber (ROSS et al. 2000), the Upper Cretaceous ambers of Taimyr (Russia) (EVANS 1973) and New Jersey (USA) (GRIMALDI 2000), the Upper Cretaceous lacustrine Orapa deposit (Botswana) (BROTHERS et al. 1993), the Lower Cretaceous amber of Álava (Spain) (MARTÍNEZ-DELCÓS et al. 1999), and the Lower Cretaceous Lebanese amber (PRENTICE, 1993, 1994). Nevertheless the discovery in the Early Eocene amber of Oise of a new genus of Bethylinae is the oldest representative of this subfamily. Three new fossils of the subfamily Epyrinae are also reported. They were described as *Rhabdopyris gallicus* – earliest known representative of this modern genus (Fig. 4B), the new genus and species *Elektroepyrus magnificus*, and an undetermined Epyrini. The new fossils emphasise the high diversity of the subfamily Epyrinae during the Eocene (PERRICHOT & NEL 2008).

The Dryinidae is a small family of parasitic wasps, their fossil record is rather abundant with 34 described species from amber ranging from the Early Cretaceous (Lebanon) to the Miocene (Dominican Republic) (OLMI 1984; OLMÍ et al. 2001; ENGEL 2003).

Fossil Ichneumonidae are frequently found. BRUES (1910a) listed 12 genera in the Baltic amber and 34 genera in the Oligocene Florissant Shales (USA), while STATZ (1938) listed 124 species from eight lacustrine outcrops ranging from the Eocene to the Miocene, and only 15 species from the Upper Eocene Baltic amber. Currently c. 190 species have been described (MENIER et al. 2004).

The description of the first fossil representative of the subfamily Metopiinae, discovered in the Early Eocene amber of Oise, shows the great importance of this deposit and supports the hypothesis of a high diversity of the Ichneumonidae throughout the Cenozoic (MENIER et al. 2004).

Bees are very rare in fossil deposits (MICHENER 2007). Worldwide, four main deposits of bee fossils are known: Dominican amber from the Miocene (20 Myr),

Florissant shale from the Eocene-Oligocene boundary (34 Myr), as well as the Eckfeld/Messel shales and Baltic amber from the Middle Eocene (c. 45 Myr). These sources have produced sizeable bee palaeofaunas showing unexpected taxonomic Paleogene bee diversity (ZETUNER & MANNING 1976; POINAR 1999; ENGEL 2001; WAPPLER & ENGEL 2003). Cretaceous, Paleocene and Early Eocene bee fossils are much rarer. Only six specimens have been found in layers older than 50 Myr (MICHEZ et al., in press). *Paleomacropis eocenicus* MICHEZ & NEL, 2007 from Oise amber is the oldest record of the melittid bee and the fifth oldest fossil in the entire bee group (Fig. 4D). The discovery of an early Eocene Melittidae supports the hypothesis that Melittidae could constitute the basal group of the bee clade (MICHEZ et al. 2007; DANFORTH et al. 2006).

Scelionidae are divided into three subfamilies (Scelioninae, Teleasinae, Telenominae) and contain about 150 genera with about 3000 extant species (GOULET et al. 1993). Many undescribed specimens of Scelionidae were indicated (ARBIZU 1999; ENGEL 2000; MARTÍNEZ-DELCÓS et al. 1998), however, Scelionidae belongs to the more frequent group of Hymenoptera in Baltic amber primarily described by BRUES (1940).

Scolebythidae constitute a very small family with only three modern genera (LACAU et al. 2000). PRENTICE et al. (1996) described two fossil scolebythids from the Lebanese Lower Cretaceous and Miocene Dominican ambers, BROTHERS et al. (1998) mentioned a Scolebythidae from the Upper Eocene Baltic amber, and AZEVEDO (1999) described an extant species from Brazil.

The oldest representatives of the sphecid tribe Trypoxylini are described from the Early Eocene of Oise (Fig. 4E) (NEL 2005). Tripoxylini are very frequent and diverse in the Oise amber, representing about 10% of the arthropod inclusions!

## Isoptera

The diversity of this order in the Paleocene-Eocene is nowadays mainly known from Baltic amber. There is some additional records from the Middle Eocene of Ukraine, Germany and Canada (NEL et al. 1993). The Oise amber comprises a Kalotermitidae and a Mastotermitidae (Fig. 4F) (NEL & BOURGUET 2006). These authors supposed that the presence of the latter family in the Oise amber and its supposed absence in the Baltic amber could have been related to different plant origins of the resins, but ENGEL et al. (2008) recently discovered the family Mastotermitidae in the Baltic amber.

## Lepidoptera

These are mainly moths of very small size, with a probably high diversity. The families Gelechiidae, Oe-

cophoridae, Tineidae have been recognised, but the whole fauna is still to study.

### Mantodea

Several fragments of large Mantodea (fore legs, fragments of antenna, body parts) have been collected. The few more complete specimens represent three or four species, with one very remarkable taxon with a short prothorax.

### Megaloptera

Megaloptera specimens are rare in ambers, thus the description of an adult Sialidae in the Early Eocene amber of Oise is of great interest for the analysis of the past biodiversity of this order (NEL et al. 2001).

### Neuroptera

Two taxa have been described from the Early Eocene ambers of Oise, a new genus and species of Sisyridae and Rhachiberothidae (NEL et al. 2003a, NEL et al. 2005a). Sisyridae includes only five extant genera. JARZEMBOWSKI (1980) described a fossil Sisyridae from the Upper Eocene of the Isle of Wight (UK), WICHARD & WEITSCHAT (1996) figured two adult specimens from the Baltic amber, WEITSCHAT & WICHARD (1998) also figured a female adult specimen from the Baltic amber, and SCHUMANN & WENDT (1989) mentioned a fossil Sisyridae from the Saxonian amber (Miocene, Germany). Some fossil specimens of *Paleosisyra eocenica* are covered by pollen, suggesting that it lived on flowers (NEL et al. 2003).

The Rhachiberothidae is a very small neuropteran family of three extant genera restricted to the eastern and southern parts of Africa (ASPÖCK et al. 1997), it could be indicative of a sub-tropical to dry temperature palaeoclimate. SCHLÜTER (1978) described one specimen from the Cenomanian amber from Bezonnaix (northwest France) and GRIMALDI (2000) one from the Turonian amber from New Jersey (USA).

### Odonata

Several fragments of Odonata wings have been discovered but only one could be described in the family Libellulidae (FLECK et al. 2000).

### Orthoptera

Several fragments of legs and bodies have been found. Two specimens of a Tridactylidae belong to the new genus and species *Guntheridactylus grimaulti* (Fig. 3C). It is the second oldest definitive representative of the modern tridactylid lineage (AZAR & NEL 2008; HEADS 2009).

### Psocoptera

The Eocene psocopteran fauna from the amber of Oise is shown to be very diverse with 10 recorded families, 11 species and four new genera (Fig. 3B) (NEL et al. 2005). Nevertheless, the Psocoptera fossil record remains rather scarce despite papers on the Cretaceous amber faunas (BAZ et al. 2000, 2001a, b; PERRICHOT et al. 2003). The Psocoptera have been poorly known in the Paleocene-Eocene boundary, but the French Early Eocene amber of Oise partly fills this gap.

### Thysanoptera

A rich fauna of Thysanoptera has been found all corresponding to new species (Fig. 4A). Five new genera, and 13 new species were recognized in Melanthripidae, Thripidae, and in Phlaeothripidae, which represents the oldest accurate record of Tubulifera. The Oise amber thrips fauna has few affinities with that of the Baltic amber, and indicates a warm palaeoclimate, in agreement to other analyses of the invertebrates, the vertebrates, and the plants of this outcrop (NEL et al., in press).

### Trichoptera

Several large adult specimens have been found. At this stage it is nearly impossible to estimate the number of different species.

## Discussion

With 49 recorded families and 79 described species, the amber deposits of Oise is less diverse than more important deposits like Baltic, Dominican or New Jersey ambers. However, the Oise deposit is exceptional in covering a period devoid of other amber discoveries. The discovery of new taxa in the Early Eocene amber of Oise is of great phylogenetic interest and allows a better understanding of the past diversity.

The closest deposit from Oise deposit is in time and localisation the Baltic amber. But there are very few shared species between the Oise and younger Baltic amber (NEL et al. 2005b). We have an angiosperm origin for the Oise amber and a Gymnosperm origin for the Baltic amber. This difference of origin may partly reflect the differences of fauna between these two deposits. Nevertheless it is necessary to remain very prudent with the non-discovery of a taxon in a fossil assemblage. The family Mastotermitidae remained unknown in the Baltic amber until its very recent discovery by ENGEL et al. (2008). Another hypothesis to explain these differences is to evoke the Eocene climatic degradation. Several taxa of the Oise amber show affinities with taxa now living in very warm environments. This needs to be confirmed through future analyses of the still unstudied orders.



## Zusammenfassung

In dieser Arbeit wird über den aktuellen Stand der Forschung der Insektenfauna aus dem eozänen Bernstein von Oise (Frankreich) berichtet. Obwohl mehrere Ordnungen bereits gründlich bearbeitet wurden, harren noch viele Gruppen einer Bearbeitung. Dies gilt insbesondere für die Lepidoptera, Trichoptera, Ephemeroptera und Blattodea, welche zumal für eine Rekonstruktion der Paläo-Umwelt von Bedeutung sind. Momentan sind nur wenige Taxa bekannt, die sowohl im Oise Bernstein als auch im Baltischen Bernstein vorkommen. Dies, so wird vermutet, könnte mit einer schnellen Evolutionsrate der Insekten zusammenhängen, ausgelöst durch die großen, globalen Klimaveränderungen nach dem Wärme-Optimum im späten Paläozän.

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## References

- ARBIZU M., E. BERNÁRDEZ, E. PEÑALVER & M.A. PRIETO (1999): El ambar de Asturias (España). — *Estud. Mus. Cienc. Nat. Alava* **14**: 245-254.
- ARILLO A. & A. NEL (2000): Two new fossil cecidomyiids flies from the Lower Cretaceous amber of Alava (Spain) (Diptera, Cecidomyiidae) — *Bull. Soc. entomol. France* **105**: 285-288.
- AMORIM D.S. (1998): Amber fossil Scatopsidae 1. Considerations on described taxa, *Procolobostema roseri* n. sp. from Dominican amber, and the position of Procolobostema in the family — *American Mus. Nov.* **3227**: 1-17.
- ASPÖCK U. & H. ASPÖCK (1997): Studies on new and poorly-known Rachiberothidae (Insecta: Neuroptera) from subsaharan Africa — *Ann. Naturhist. Mus. Wien* **99**: 1-20.
- AZAR, D. & A. NEL (2008). First Tridactylidae from the Eocene French amber (Insecta: Orthoptera). — *Alavesia* **2**: 169-175.
- AZAR, D., A. NEL, M. SOLIGNAC, J.-C. PAICHELER & F. BOUCHET (1999): New genera and species of psychodoid flies from the Lower Cretaceous amber of Lebanon — *Palaeontology* **42**: 1101-1136.
- AZEDO C.O. (1999): A key to world species of Scolebythidae with description of a new species of Dominibythus from Brazil — *J. Hymenoptera Res.* **8**: 1-5.
- BATELKA J., F.-M. COLLOMB & A. NEL. (2006): *Macroisagon deuvei* n.sp. (Coleoptera: Ripiphoridae) from the French Eocene amber — *Ann. Soc. entomol. France (n.s.)* **42** (1): 75-78.
- BAZ A. & V.M. ORTUÑO (2000): Archaeatropidae, a new family of Psocoptera from the Cretaceous amber of Alava, Northern Spain — *Ann. Entomol. Soc. America* **93**: 367-373.
- BAZ A. & V.M. ORTUÑO (2001a): New genera and species of empheriids (Psocoptera: Empheriidae) from the Cretaceous amber of Alava, Northern Spain — *Cret. Res.* **22**: 575-584.
- BAZ A. & V.M. ORTUÑO (2001b): A new electrentomoid psocid (Psocoptera) from the Cretaceous amber of Alava (Northern Spain) — *Mitt. Mus. Naturk. Berlin, Deutsche Entomol. Z.* **48**: 27-32.
- BECHLY G. & M. WITTMANN (2000): Two new tropical bugs (Insecta: Heteroptera: Thaumastocoridae-Xylastodorinae and Hysipterygidae) from Baltic amber — *Stuttgarter Beitr. Naturk.* **289**: 1-11.
- BROTHERS D.J. & R.J. RAYNER (1993): Mesozoic aculeate Hymenoptera from Orapa, Botswana — *Proc. 9th Entomol. Congr. Entomol. Soc. Southern Africa*: 132.
- BROTHERS D.J. & J.W. JANZEN (1998): Review of Scolebythidae (Hymenoptera: Chrysidoidea) with description of a new species of *Dominibythus* from Baltic amber — 1<sup>st</sup> Paleontomol. Conf., Abstracts, 30 Aug. – 4 Sept. 1998, Moscow: 4.
- BRUES C.T. (1910a): Some notes on the geological history of the parasitic Hymenoptera — *J. New York Entomol. Soc.* **18** (1): 1-22.
- BRUES C.T. (1932): The parasitic Hymenoptera of the Baltic amber. Part 1 — *Bernstein-Forsch. (Amber studies)* **3**: 4-179.
- BRUES C.T. (1940): Fossil parasitic Hymenoptera of the family Scelionidae from Baltic amber — *Proc. American Acad. Arts Sci., Boston* **74**: 69-90.
- DANFORTH B.N., S.D. SIPES, J. FANG & S.G. BRADY (2006) - The history of early bee diversification based on five genes plus morphology. — *Proc. Nat. Acad. Sci. USA* **103**: 15118-15123.
- DE FRANCESCHI D. & G. DE PLOËG (2003): Origine de l'ambre des faciès sparnaciens (Eocène inférieur) du bassin de Paris: le bois de l'arbre producteur — *Geodiversitas* **25** (4): 663-647.
- DE PLOËG G. & A. NEL (2004): A new bethylid wasp from the Lowermost Eocene amber of France (Hymenoptera: Bethylinidae: Bethylinae) — *Geol. Acta* **2** (1): 75-82.
- ENGEL M.S. (2000): A new interpretation of the oldest fossil bee (Hymenoptera: Apidae) — *American Mus. Nov.* **3296**: 1-11.
- ENGEL M.S. (2001): A monograph of the Baltic Amber bees and evolution of the Apoidea (Hymenoptera) — *Bull. American Mus. Nat. Hist.* **259**: 1-192.
- ENGEL M.S. (2003): An anteonine wasp in Cenomanian-Albian amber from Myanmar (Hymenoptera: Dryinidae) — *J. Kansas Entomol. Soc.* **76** (4): 616-621.
- ENGEL M.S., D.A. GRIMALDI & K. KRISHNA (2008). A synopsis of Baltic amber termites (Isoptera) — *Stuttgarter Beitr. Naturk., (B)* **372**: 1-20.
- EVANS H.E. (1973): Cretaceous aculeate wasps from Taymir, Siberia (Hymenoptera) — *Psyche* **80** (3): 166-178.
- EVENHUIS N.L. (1991): World catalog of genus-group names of bee flies (Diptera: Bombyliidae) — *Bishop Mus. Bull. Entomol.* **5**: 1-105.
- EVENHUIS N.L. (1994): Catalogue of the fossil flies of the world (Insecta: Diptera) — *Backhuys Publs, Leiden*.
- FEDOTOVA Z.A. & E.E. PERKOVSKI (2004): New gall midges (Diptera: Cecidomyiidae) from the Rovno amber: subfamily Lestremiinae, tribes Strobliellini and Campylomyzini; subfamily Porricondyliinae, tribes Diadocidiini and Asynaptini — *Paleontol. J.* **38** (5): 538-547.
- FEDOTOVA Z.A. & E.E. PERKOVSKI (2005): New gall midges (Diptera: Cecidomyiidae) from the Rovno amber: subfamily Porricondyliinae (tribes Bryocryptini and Winnertziini) and subfamily Lasiopterinae (tribes Brachineurini and Oligotrophini) — *Paleontol. J.* **39** (1): 41-51.

- FLECK G., A. NEL, G. DE PLOËG & G. MASSELOT (2000). New fossil dragonfly from the Lowermost Eocene amber of France (Insecta, Odonata, Anisoptera) — *Acta Geol. Hispanica* **35** (1-2): 131-134.
- GORDH G. & L. MOCZAR (1990): A catalog of the world Bethyliidae (Hymenoptera: Aculeata) — *Mem. American Entomol. Inst.* **46**: 1-364.
- GAGNÉ R.J. (1973): Cecidomyiidae from Mexican Tertiary amber (Diptera) — *Proc. Entomol. Soc. Washington* **75**: 169-171.
- GAGNÉ R.J. (1977): Cecidomyiidae (Diptera) from Canadian amber — *Proc. Entomol. Soc. Washington* **79** (1): 57-62.
- GEE J., A. NEL, J.-J. MENIER & G. DE PLOËG (2001): A new lovebug fly (Insecta, Diptera) from the lowermost Eocene amber of the Paris Basin — *Geodiversitas* **23** (3): 341-348.
- GOULET H. & J.T. HUBER (1993): Hymenoptera of the world: an identification guide to families — *Res. Branch Agricult. Canada Publ., Ottawa* **1894/E**: 65-100.
- GRIMALDI D.A. & J. CUMMING (1999): Brachyceran Diptera in Cretaceous ambers and Mesozoic diversification of the Eremoneura — *Bull. American Mus. Nat. Hist.* **239**: 124 pp.
- GRIMALDI D.A. (2000): Studies of fossils in amber, with particular reference to the Cretaceous of New Jersey — Backhuys Publishers, Leiden.
- GRIMALDI D.A., M.S. ENGEL & P.D. NASCIBENE (2002): Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance — *American Mus. Nov.* **3361**: 1-71.
- HARRINGTON G.J. & C. JARAMILLO (2003): Paratropical floral extinction in the Late Paleocene-Early Eocene — *J. Geol. Soc.* **164** (2): 323-332.
- HEADS S. (2009): A new pygmy mole cricket in Cretaceous amber from Burma (Orthoptera: Tridactylidae) — *Denisia* **26**: 75-82.
- JARZEMBOWSKI E.A. (1980): Fossil insects from the Bembridge Marls, Paleogene of the Isle of Wight — *Bull. British Mus. Nat. Hist.* **33**: 237-293.
- KAUPP A., Z. FALIN & P. NAGEL (2001): An annotated catalogue of fossil Ripiphoridae, taxonomic notes, and the description of a new genus and species from Baltic amber (Coleoptera: Ripiphoridae: Ripidiinae) — *Mitt. Geol.-Paläontol. Inst. Univ. Hamburg* **85**: 165-195.
- KIREJTSHUK A.G. & A. NEL (2008). New taxa of Polyphaga from the Lowermost Eocene French amber (Insecta: Coleoptera). — *Ann. Soc. entomol. France* **44**(4): 419-442.
- KIREJTSHUK A.G., A. NEL & F.-M. COLLOMB (in press). New Archostemata (Insecta, Coleoptera) from the French Paleocene and Early Eocene. — *Ann. Soc. entomol. France*.
- KROMBEIN K.V. (1992): Systematics of the genera of Epyrinae with ramose male antennae (Bethyliidae, Hymenoptera) — *Proc. Entomol. Soc. Washington* **94**: 345-360.
- LACAU S., A. NEL, C. VILLEMANT, J.-J. MENIER, M.J. ORLAC & G. DE PLOËG (2000): A Fossil Scolythyidae from the Lowermost Eocene Amber of France (Insecta: Hymenoptera) — *Ann. Entomol. Soc. America* **93** (4): 701-706.
- LEFEBVRE F., T. BOURGOUIN & A. NEL (2007): New Cixiidae and Achilidae fossils from the Middle Eocene Baltic amber (Hemiptera: Fulgoromorpha) — *Ann. Soc. entomol. France (n.s.)* **43** (1): 37-43.
- MARTÍNEZ-DELCOX X. & E. PEÑALVER-MOLLA (1998): The fossil Scelionidae (Insecta: Hymenoptera) from the Lower Cretaceous Amber of Álava (Spain) — *World Congr. Amber Inclusions. 20-23 October 1998, Vitoria-Gasteiz, Álava*: 163.
- MARTÍNEZ-DELCOX X., A. ARILLO, V. ORTUÑO & E. PEÑALVER-MOLLA (1999): El ámbar del Cretácico Inferior de Peñacerrada (Álava, Spain) — *Temas Geol.-Min.* **2**: 13-17.
- MENIER J.-J., A. NEL, A. WALLER & G. DE PLOËG (2004): A new fossil Ichneumon wasp from the Lowermost Eocene amber of Paris Basin (France), with a checklist of fossil Ichneumonidae S.L. (Insecta: Hymenoptera: Ichneumonidae: Metopinae) — *Geol. Acta* **2** (1): 83-94.
- MEUNIER F. (1899): Révision des Diptères fossiles types de Loew — *Misc. Entomol.* **7**: 1-17.
- MEUNIER F. (1904): Monographie des Cecidomyiidae, Sciaridae, Mycetophilidae et Chironomidae de l'ambre de la Baltique — *Ann. Soc. sci. Bruxelles* **28**: 13-276.
- MEUNIER F. (1907): Beitrag zur Fauna der Bibioniden, Simuliden, und Rhyphiden des Bernsteins — *Jb. königl. Preussischen Geol. Landesanst. Bergakad. Berlin* **24**: 391-404.
- MICHENER C.D. (2007): The bees of the world (2<sup>nd</sup> edition). — The Johns Hopkins University Press, Baltimore.
- MICHEZ D., A. NEL, J.-J. MENIER & P. RASMONT (2007): The oldest fossil of a melittid bee (Hymenoptera: Apiformes) from the Early Eocene of Oise (France) — *Zool. J. Linnean Soc.* **150**: 701-709.
- MICHEZ D., T. DEMEULEMEESTER, A. NEL, P. RASMONT & S. PATINY (in press): New fossil evidence of the early diversification of bees: *Paleohabropoda oudardi* from the French Paleocene (Hymenoptera, Apidae, Anthophorini) — *Zool. Scr.*
- NEL A. (2005): Oldest representatives of the Sphecidae: Trypoxylini in the Early Eocene French amber (Insecta: Hymenoptera) — *C. R. Palevol* **4**: 17-24.
- NEL A. (2006): Oldest records of Bombyliidae: Phthiriinae and Mythicomyiidae: Glabellulinae from the lowermost Eocene amber of France (Diptera: Bombylioidea) — *European J. Entomol.* **103**: 109-114.
- NEL A. & E. BOURGOUIN (2006): Termite of the Early Eocene amber of France (Isoptera: Mastotermitidae: Kalotermitidae) — *N. Jb. Geol. Paläontol. Monatsh.* **2**: 101-115.
- NEL A. & G. DE PLOËG (2004): New fossil bee flies (Diptera: Bombylioidea) in the Lowermost Eocene Amber of the Paris Basin — *Geol. Acta* **2** (1): 57-65.
- NEL A. & J.-C. PAICHELER (1993): Les Isoptera fossiles (Insecta: Dictyoptera) — *Cah. Paléontol.* **1993**: 102-179.
- NEL A. & J.F. PETRULVICIUS (2003): New Paleogene bees from Europe and Asia — *Alcheringa* **27**: 227-293.
- NEL A. & J. PROKOP (2004): New Palaeogene Scatopsidae (Diptera: Nematocera) in amber from the Czech Republic and France — *Acta Soc. Zool. Bohemicae* **68**: 91-98.
- NEL A. & J. PROKOP (2005): New fossil Scelionidae (Insecta: Hymenoptera) in Early Paleogene amber from eastern Moravia (Czech Republic) and northern France — *Polish J. Entomol.* **74**: 339-347.
- NEL A. & J. PROKOP (2006): New fossil gall midges from the earliest Eocene French amber (Insecta, Diptera, Cecidomyiidae) — *Geodiversitas* **28** (1): 37-54.
- NEL A., V. ALBOUY, C. CAUSSANEL & C. JAMET (1994): Réflexion paléo-entomologique sur la systématique des Dermaptères. Quatre nouveaux forficules fossiles de l'Oligocène de Provence (France) (Dermaptera) — *Bull. Soc. entomol. France* **99**: 253-266.

- NEL A., G. DE PLOËG, J. DEJAX, D. DUTHEIL, D. DE FRANCESCHI, E. GHEERBRANT, M. GODINOT, S. HERVET, J.-J. MENIER, M. AUGÉ, G. BIGNOT, C. CAVAGNETTO, S. DUFFAUD, J. GAUDANT, S. HUA, A. JOSSANG, F. DE LAPPARENT DE BROIN, J.-P. POZZI, J.-C. PAICHELER, F. BOUCHET & J.-C. RAGE (1999): Un gisement sparnacien exceptionnel à plantes, arthropodes et vertébrés (Éocène basal, MP7): Le Quesnoy (Oise, France) — C. R. Acad. Sci., Sci. terre plan. **329**: 65-72.
- NEL A., J.-J. MENIER, G. DE PLOËG, G. HODEBERT & L. DANVIN (2001): *Eosialis*, a new alderfly genus in French Lowermost Eocene amber (Insecta: Megaloptera: Sialidae) — Geobios **35**: 313-319.
- NEL A., J.-J. MENIER & G. DE PLOËG (2002): The oldest representative of the Trichomyiinae from the Lowermost Eocene Amber of the Paris Basin (France) (Diptera: Psychodidae) — Ann. Soc. entomol. France (n.s.) **38** (3): 247-252.
- NEL A., J.-J. MENIER, A. WALLER, G. HODEBERT & G. DE PLOËG (2003a): New fossil spongilla-flies from the Lowermost Eocene amber of France (Insecta: Neuroptera: Sisyridae) — Geodiversitas **25** (1): 109-117.
- NEL A., A. WALLER, V. ALBOUY, J.-J. MENIER & G. DE PLOËG (2003b): New fossil earwigs from the lowermost Eocene amber of the Paris Basin (France) (Insecta, Dermaptera, family incertae sedis) — Geodiversitas **25** (1): 119-129.
- NEL A., G. DE PLOËG & D. AZAR (2004a): The oldest Liposcelididae in the Lowermost Eocene amber of the Paris Basin (Insecta: Psocoptera) — Geol. Acta **2** (1): 67-74.
- NEL A., G. DE PLOËG, J. MILLET, J.-J. MENIER & A. WALLER (2004b): The french ambers: a general conspectus and the Lowermost Eocene amber deposit of Le Quesnoy in the Paris Basin — Geol. Acta **2** (1): 3-8.
- NEL A., A. WALLER & G. DE PLOËG (2004c): The oldest fossil psamatid bug in the Lowermost Eocene amber of the Paris Basin (Heteroptera: Lygaeoidea: Piesmatidae) — Geol. Acta **2** (1): 45-50.
- NEL A., A. WALLER & G. DE PLOËG (2004d): The oldest fossil Tingidae from the Lowermost Eocene amber of the Paris Basin (Heteroptera: Cimicomorpha: Tingioidea) — Geol. Acta **2** (1): 37-43.
- NEL A., A. WALLER & G. DE PLOËG (2004e): The oldest palm bug in the Lowermost Eocene amber of the Paris Basin (Heteroptera: Cimicomorpha: Thaumastocoridae) — Geol. Acta **2** (1): 51-55.
- NEL A., A. WALLER & G. DE PLOËG (2004f): An aulacid wasp in the Lowermost Eocene amber from the Paris Basin (Hymenoptera: Aulacidae) — Geol. Acta **2** (1): 67-74.
- NEL A., V. PERRICHOT, D. AZAR & D. NÉRAUDEAU (2005a): New Rhachiberothidae (Insecta: Neuroptera) in Early Cretaceous and Early Eocene ambers from France and Lebanon — N. Jb. Geol. Paläontol. Monatsh. **235**: 51-85.
- NEL A., J. PROKOP, G. DE PLOËG & J. MILLET (2005b): New Psocoptera (Insecta) from the Lowermost Eocene amber of Oise, France — J. Syst. Palaeontol. **3** (4): 371-391.
- NEL P., D. AZAR, A. SALLOUM & A. NEL (in press): Thysanoptera of the lowermost Eocene French amber (Insecta) — Ann. Soc. Entomol. France.
- OHL M. (1995): A new species of Bethylinidae of the genus *Lyp-topsenella* Kieffer, 1991 from Baltic amber — Paläontol. Z. **69**: 409-416.
- OLMI M. (1984): A revision of the Dryinidae (Hymenoptera) — Mem. Entomol. Inst. **37**: 1-1913.
- OLMI M. & G. BECHLY (2001): New parasitic wasps from Baltic amber (Insecta: Hymenoptera: Dryinidae) — Stuttgarter Beitr. Naturk. **306**: 1-58.
- PEARSON P.N., P.W. DITCHFIELD, J. SINGANO, K.G. HARCOURT-BROWN, C.J. NICHOLAS, R.K. OLSSON, N.J. SHACKLETON & M.A. HALL (2001): Warm tropical sea surface temperatures in the Late Cretaceous and Eocene epochs — Nature **413**: 481-487.
- PEINADO J., A. NEL & A. WALLER (2006): A dryinid wasp in the Early Eocene amber from the Paris Basin (Hymenoptera: Dryinidae) — Zootaxa **1168**: 31-41.
- PERKOVSKI E.E. & Z.A. FEDOTOVA (2004): New species of gall midges (Diptera: Cecidomyiidae) from Rovno amber: subfamily Lestremiinae, tribes Micromyiini and Peromyiini — Paleontol. J. **38** (4): 396-406.
- PERRICHOT V. & A. NEL (2008). Eocene bethylid wasps from French amber (Hymenoptera: Bethylinidae) — N. Jb. Geol. Paläontol., Abh. **248** (1): 91-101.
- PERRICHOT V., D. AZAR, D. NÉRAUDEAU & A. NEL (2003): New Psocoptera in the Lower Cretaceous ambers of Southwestern France and Lebanon (Insecta: Psocoptera: Trogiomorpha) — Geol. Mag. **140**: 669-683.
- PERRICHOT V., A. NEL & D. NÉRAUDEAU (2004): Two new wedge-shaped beetles in Alo-Cenomanian ambers of France (Coleoptera: Ripiphoridae: Ripiphorinae) — Australian J. Zool. **3**: 71-94.
- PERRICHOT V., A. NEL, E. GUILBERT & D. NÉRAUDEAU (2006). Fossil Tingioidea (Heteroptera: Cimicomorpha) from French Cretaceous amber, including Tingidae and a new family, Ebboidae — Zootaxa **1203**: 57-68.
- PIKE E.M. (1994): Historical changes in insect community structure as indicated by hexapods of Upper Cretaceous Alberta (Grassy Lake) amber — Canadian Entomol. **126**: 695-702.
- POLASZEK A. & K.V. KROMBEIN (1994): The genera of Bethylinae (Hymenoptera: Bethylinidae) — J. Hymenoptera Res. **3**: 91-105.
- POINAR G.O. & J.A. SANTIAGO-BLAY (1997): *Paleodoris lattini* gen.n., sp.n., a fossil palm-bug (Thaumastocoridae, Xylostodoridae) in Dominican amber, with habits discernible by comparative functional morphology — Entomol. Scand. **28**: 307-310.
- POINAR G.O. (1999): Cenozoic fauna and flora in amber — Estud. Mus. Cienc. Nat. Alava **14**: 151-154.
- POINAR G.O. & R. MILKI (2001): Lebanese amber. The oldest ecosystem in fossilized resin — Oregon State University Press, Corvallis.
- PRENTICE M.A. (1993): Early Cretaceous Aculeata from Lebanese amber — Sphecos **26**: 8.
- PRENTICE M.A. (1994): Some further notes on Lebanese Aculeata — Sphecos **27**: 12.
- PRENTICE M.A., G.O. POINAR & R. MILKI (1996): Fossil Scolebythids (Hymenoptera: Scolebythidae) from Lebanese and Dominican amber — Proc. Entomol. Soc. Washington **98**: 802-811.
- RASNITSYN A.P. & A.J. ROSS (2000): A preliminary list of arthropod families present in the Burmese amber collection at the Natural History Museum, London — Bull. Nat. Hist. Mus., London, Geol. **56** (1): 21-24.
- ROSS A.J. & P.V. YORK (2000): A list of type and figured specimens of insects and other inclusions in Burmese amber — Bull. Nat. Hist. Mus., London, Geol. **56** (1): 11-20.



- SCHLÜTER T. (1984): Zur Systematik und Palökologie harzkonserverter Arthropoda einer Taphozönose aus dem Cenomanium von NW-Frankreich — *Berliner Geowiss. Abh.*, (A) **9**: 1-150.
- SCHUMANN H. & H. WENDT (1989): Zur Kenntnis der tierischen Inkluden des sächsischen Bernstein — *Deutsche Entomol. Z.* **36**:33-44.
- SLATER J.A. & R.M. BARANOWSKI (2000): *Discocoris dominicanus*, a new species of palm bug from Dominican amber (Heteroptera: Thaumastocoridae) — *Florida Entomol.* **83**: 349-353.
- STATZ G. (1938): Neue Funde parasitischer Hymenoptera aus dem Tertiär von Rott am Siebengebirge — *Decheniana* **98** (1): 71-154.
- SZWEDO J., T. BOURGOUIN & F. LEFEBVRE (2006): New Mnemosynini taxa (Hemiptera, Fulgoromorpha: Cixiidae) from the Palaeogene of France with notes on their early association with host plants — *Zootaxa* **1112**: 31-41.
- WAPPLER T. & M.S. ENGEL (2003): The Middle Eocene bee faunas of Eckfeld and Messel, Germany (Hymenoptera: Apoidea) — *J. Paleontol.* **77**: 908-921.
- WICHARD W. & W. WEITSCHAT (1998): Atlas der Pflanzen und Tiere im Baltischen Bernstein — Pfeil Verlag, München.
- WICHARD W. & W. WEITSCHAT (1996): Wasserinsekten im Bernstein. Eine paläobiologische Studie — *Entomol. Mitt. Löbbecke Mus. + Aquazoo* **4**: 1-122.
- ZEUNER F.E. & F.J. MANNING (1976): A monograph on fossil bees (Apoidea) — *Bull. British Mus. (Nat. Hist.)*, Geol. **37**: 149-268.

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